A revised concept of landscape equilibrium: Disturbance and stability on scaled landscapes

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Abstract

Temporal and spatial scales of disturbance and recovery are often confounded in discussions of landscape equilibrium. We developed a broad framework for the description of landscapes that separates the spatial and temporal scales of disturbance and recovery and predicts the resultant dynamics of a landscape. Two key parameters representing time and space are used to describe potential disturbance dynamics. The temporal parameter, T, is the ratio of the disturbance interval (i.e., time between successive disturbance events) to the time required for a disturbed site to recover to a mature stage. The spatial parameter, S, is the ratio of the size of the disturbance to the size of the landscape. The use of ratios in both parameters permits the comparison of landscapes across a range of spatial and temporal scales. A simple simulation model was developed to explore the implications of various combinations of S and T. For any single simulation, disturbances of a fixed size are imposed at random locations on a gridded landscape at specified intervals. Disturbed sites recover deterministically through succession. Where disturbance interval is long relative to recovery time and a small proportion of the landscape is affected, the system is stable and exhibits low variance over time (e.g., northeastern hardwood forests). These are traditional "equilibrium" systems. Where disturbance interval is comparable to recovery interval and a large proportion of the landscape is affected, the system is stable but exhibits large variance (e.g., subalpine forests in Yellowstone Park). Where disturbance interval becomes much shorter than recovery time and a large proportion of the landscape is affected, the system may become unstable and shift into a different trajectory (e.g., arid ecosystems with altered fire regimes). This framework permits the prediction of disturbance conditions that lead to qualitatively different landscape dynamics and demonstrates the scale-dependent nature of concepts of landscape equilibrium.

Introduction

The notion of equilibrium in ecological systems has inspired a long history of interest and controversy in ecology (e.g., Egerton 1973; Bormann and Likens 1979; Connell and Sousa 1983; Wiens 1984; DeAngelis and Waterhouse 1987). A belief in the orderliness of the universe is deeply woven into the fabric of western culture (Botkin 1990), and this classical view holds that the existence of an equilibrium state is probable. Certainly, a paradigm of orderliness underlies current concepts of landscape equilibrium. However, concepts of orderliness and equilibrium are confounded by problems of scale, and landscapes can exhibit a suite of dynamics of which equilibrium is but one. The controversy regarding equilibrium stems in part from the inconsistent definitions and criteria

used by investigators and in part from the question of whether it is valid to define the existence of an equilibrium state at all. DeAngelis and Waterhouse (1987) examine these arguments in an excellent review of equilibrium and nonequilibrium concepts in ecological models. In this paper, we address the concept of landscape equilibrium by first clarifying its usage in ecology, then presenting a broad context for the description of landscapes. This framework is illustrated by a simple model that incorporates the space and time scales of disturbance and predicts the resultant dynamics of a landscape across a range of scales, permitting space and time to be considered independently.

The term scale is used in many different ways and may connote different aspects of space and time. Scale refers to the spatial or temporal dimension of an object or process and is characterized by both grain and extent (Allen and Starr 1982; O'Neill *et al.*, 1986; Wiens 1989; Turner *et al.* 1989a). Grain refers to the finest level of spatial or temporal resolution within a given data set (e.g., cell size in a gridded landscape). Extent refers to the size of the study area or the duration of time under consideration. Changes in the meaning of 'scale' from grain to extent can have important qualitative and quantitative effects on how landscape measurements change across scales (Turner *et al.* 1989b). In this paper, we deal solely with the extent component of scale.

Equilibrium points can be precisely defined mathematically, but equilibrium and stability are not well defined when applied to real ecological systems (DeAngelis and Waterhouse 1987). The properties that have been used to evaluate equilibrium fall into two general categories: persistence (i.e., simple non-extinction) and constancy (i.e., no change or minimal fluctuation in numbers, densities, or relative proportions). Persistence might be applied to all species, as emphasized in many population-oriented models (e.g., DeAngelis and Waterhouse 1987), or the presence of all stand age classes or successional stages in a landscape (e.g., Romme 1982). Constancy may refer to the number of species (e.g., MacArthur and Wilson 1967), the density of individual species (e.g., May 1973), the standing crop of biomass (e.g., Bormann and Likens 1979; Sprugel 1985), or the relative propor-

tions of seral stages on a landscape (e.g., Romme 1982; Baker 1989a, b). There are fundamental differences in considering species composition versus structural attributes such as biomass, age classes, and seral stages. Seral stages or age classes do not become extinct because they can be regenerated by disturbances, provided their component species do not become extinct. In addition, the structural attributes do not compete, except possibly in a temporal sense as one seral stage replaces a previous one. In this paper, we focus on the distributions of seral stages in considering equilibrium at the landscape level.

Concepts of landscape equilibrium

The simplest concept of order that might be imposed on a landscape would be equilibrium in the sense of absolute constancy, that is, there are no changes through time. However, disturbance (i.e., any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment [White and Pickett 1985]) and change are integral parts of landscape dynamics. We use disturbance in this paper to refer to any change that resets succession at one or more sites back to the earliest stage. This broad definition incorporates small disturbances, such as the death of an individual tree, as well as broad-scale events, such as fires or hurricanes. Disturbance creates patterns in vegetation by producing a patch mosaic of seral stages, and ecologists have long recognized the importance of landscape-level patch mosaics (e.g., Cooper 1913; Leopold 1933; Watt 1947; White 1979). Clearly, disturbance must be incorporated into any concept of landscape equilibrium.

Even in the absence of absolute constancy, the search for an orderly pattern can still be satisfied if some aspect of a landscape is invariant. In the shifting mosaic steady-state concept (Bormann and Likens 1979), the vegetation present at individual points on the landscape changes, but, if averaged over a sufficiently long time or large area, the proportion of the landscape in each seral stage is relatively constant, i.e., is in equilibrium. Bormann

and Likens (1979) suggested that, prior to settlement in northern hardwood forests of New England, the standing crop biomass of a watershed or other landscape unit varied slightly around a mean, although the biomass present at any small plot within the watershed fluctuated through time due to treefalls and subsequent regrowth. The shifting mosaic steady-state concept has been difficult to test empirically, but it has been suggested to apply to other systems. Studies of wave-generated fir forests in the northeastern United States have suggested a steady-state condition over the entire system despite widespread local patterns of community degradation and regeneration (Sprugel 1976; Sprugel and Bormann 1981). Zackrisson (1977) suggested that the forest mosaic in a boreal forest in northern Sweden remains unchanged, even though the spatial distribution of postfire succession is always changing.

The scale-dependent nature of the shifting mosaic concept was demonstrated when Romme (1982) failed to find equilibrium on a 7300-ha watershed on the subalpine plateau in Yellowstone National Park. Romme's 200-yr reconstruction of a landscape affected by a natural crown-fire regime documented wide fluctuations in landscape composition and diversity. The cycle of extensive fires occurring at intervals of approximately 300 yr suggested a landscape characterized by continual change. Romme concluded that this landscape is more appropriately viewed as a nonsteady-state system characterized by cyclic, long-term changes in structure and function. Romme and Despain (1989) expanded this study to an area of 129,600 ha, but still found constant fluctuation in the patch mosaic during the past 250 yrs. Similarly, Baker (1989a, b) tested for a stable patch mosaic in the 404,000-ha fire-influenced Boundary Waters Canoe Area (BWCA), but did not find a stable patch mosaic at any of five spatial scales. He suggested that the lack of a steady-state mosaic was due to (1) spatial heterogeneity in the fire-patch regime, e.g., in ignition sources, drought severity, fuel load, and fire spread probability, and (2) a mismatch in the scales of fire patches and environmental heterogeneity. Baker (1989a) concluded that the BWCA landscape was a "mosaic of different non-steady-state mosaics." Indeed, crown-fire dominated systems may gener-

ally be considered as nonequilibrium landscapes (Turner and Romme in press).

The shifting mosaic steady-state concept is problematic as a general property of landscapes. First, the concept seems to be applicable only when disturbances are small and frequent in a large area of homogeneous habitat (Pickett and White 1985). Large areas may be more likely than small areas to exhibit a stable mosaic (Zedler and Goff 1973; Connell and Sousa 1983; DeAngelis and Waterhouse 1987). Shugart and West (1981) suggested that a quasi-steady state landscape was likely only where the landscape was at least 50 times the average size of a disturbances, although Baker (1989a) failed to find equilibrium in the BWCA even at a scale 87 times the mean disturbance-patch size. Second, the concept assumes that the effects of discontinuities or gradients in topography, soils, moisture or other factors that would affect disturbance frequency or recovery are averaged across the landscape. This is a difficult condition to satisfy on real landscapes. Third, defining the sufficiently broad temporal and spatial scales over which to consider the aggregate mosaic is ambiguous. Clearly, no equilibrium exists at the scale of a few plants. If the spatial scale of analysis is expanded indefinitely, one eventually reaches the biome level. Equilibrium is again no longer relevant because different disturbance regimes and forcing functions are encountered as one crosses ecotones between biomes. Similarly, if the temporal scale is expanded indefinitely, one eventually reaches the glacial cycle and again the equilibrium is not relevant. It is well known that landscapes undergo continuous change over long time periods (e.g., Delcourt and Delcourt 1991). Paleoecological studies also suggest that the time scale of succession may overlap the time scale of paleoclimatic change (Webb 1981; Davis 1981; Delcourt *et al.* 1983). However, it is indeed conceivable to find a shifting steady-state mosaic on some landscapes at some intermediate scales, especially if there are feedback mechanisms that influence disturbance frequency (White and Pickett 1985). But, it is difficult to specify the relevant spatial and temporal scale *a priori*, and equilibrium landscapes would seem to be the exception rather than the rule (White and Pickett 1985).

Another concept considers landscape equili-

brium to be a stationary process (i.e., a stochastic process that does not change in distribution over time or space) with random perturbation (Loucks 1970). Loucks (1970) suggested that communities may appear unstable at any particular point in time because community composition is changing, but that the entire long-term sequence of changes constitutes a stable system because the same sequence recurs after every disturbance. In fire-dominated landscapes, for example, the statistical distribution of seral stages, time intervals between successive fires, or similar parameters can be determined (e.g., Van Wagner 1978; Johnson 1979; Yarie 1981; Johnson and Van Wagner 1985). This concept explicitly acknowledges the stochastic nature of disturbance, e.g., consider a probability density function for disturbance intervals of varying length (Johnson and Van Wagner 1985), but assumes that the distribution of disturbance intervals and the proportion of the landscape occupied by different seral stages remains more or less constant through time. However, the distribution of intervals between disturbances may not be the same, and the probability of disturbance may change with time since last disturbance (Clark 1989).

Patch dynamics theory (Levin and Paine 1974; Paine and Levin 1981) also focuses on interactions between disturbance and recolonization in an attempt to explain pattern dynamics in the intertidal zone. Wave-swept rocky intertidal shores are characterized by a dynamic mosaic of many species that inhabit wave-generated patches; the size distribution of these patches approximates a lognormal distribution (Paine and Levin 1981). A nonequilibrium model of patch birth and death projected total patch area accurately to within 5% of what was observed in the field (Paine and Levin 1981).

A concept related to the stationary process is that of stochastic or relative constancy through time. Botkin and Sobel (1975) suggest that a system that changes but remains within bounds is a stochastic analog of equilibrium that is much more suitable for ecological systems. Harrison (1979) also suggested that the concept of a system remaining within acceptable ranges in spite of environmental uncertainty was most relevant to ecology. However, the concept of a bounded equilibrium does not escape the problems of scale. For example, long-term monotonic changes in climate due to global warming or glacial cycles would eventually move the landscape out of pre-set bounds. And not even reasonable bounds are sufficient to envelop a spatial extent larger than a biome.

Thus, equilibrium generally has been defined relative to some "undisturbed" state. A landscape has been considered as being in equilibrium if it remains in the neighborhood (sensu Botkin and Sobel 1975) of some undisturbed state or remains balanced in the recovery stages (sensu Bormann and Likens 1979) leading to this undisturbed state. However, communities are in a constant dynamic process of adaptation to their environment such that stability (the tendency of a perturbed system to return toward this undisturbed state) may be entirely a construct appropriate to our limited powers of observation in time and space (Golley 1974).

Classic physical theory deals with stability as the monotonic recovery of a system toward equilibrium following a disturbance (e.g., May 1973). This is homeostatic stability in which the system tends to maintain the same state. Ecology, which is essentially the study of dynamic reactions to a constantly changing environment, may require the more flexible definition of homeorhesis (see O'Neill *et al.* 1986) which states that if perturbed, a system returns to its preturbation **trajectory** or rate of change. Homeorhetic stability implies return to normal **dynamics** rather than return to an artificial "undisturbed" **state.** The concept of homeorhesis permits us to deal with landscapes that are changing slowly over centuries and millenia in response to climate cycles while recovering stably over years and decades to disturbances such as fire or defoliation.

A general concept of landscape dynamics

We propose a broader view of landscape dynamics which considers the spatial-temporal scales of disturbance and the resultant landscape dynamics and can be applied across a range of scales. Of the many characteristics that can be used to describe a disturbance regime (Pickett and White 1985; Rykiel 1986), we consider four major factors character-

izing the dynamics of landscapes:

1. disturbance frequency, or its inverse, the interval between successive disturbances (e.g., Romme 1982; Baker 1989a, b);
2. rate of recovery from disturbance, or its inverse, the length of time required for a disturbed site to recover (e.g., Pickett and White 1985);
3. the size or spatial extent of the disturbance events (e.g. Bormann and Likens 1979; Shugart and West 1981; Romme 1982; Baker 1989a, b); and
4. the size or spatial extent of the landscape (e.g., Shugart and West 1981; Baker 1981a, b).

Because the functional effects of these factors are interrelated, we reduce them to two key parameters representing time and space that can be used to describe potential disturbance dynamics.

The temporal parameter (T) is defined by the ratio of the disturbance interval (i.e., the time between successive disturbances) to the recovery time (i.e., the time required for a disturbed site to achieve recovery to a "mature" stage). Defining the temporal parameter as a ratio permits the evaluation of three qualitatively different states, regardless of the type or time scale of the disturbance. These states are: (1) the disturbance interval is longer than the recovery time $(T > 1)$, so the system can recover before being disturbed again; (2) the disturbance interval and recovery time are equal ($T = 1$); and (3) the disturbance interval is shorter than the recovery time ($T < 1$), so the system is disturbed again before it fully recovers.

The spatial parameter (S) is defined by the ratio of the size of the disturbance to the size of the landscape of interest. There are two qualitatively different states of importance here, again regardless of the type of disturbance. These states are (1) disturbances that are large relative to the size of the landscape, and (2) disturbances that are small relative to the extent of the landscape. As defined in this paper, the parameter S can range from 0 to 1. The landscape dynamics cannot be predicted if the size of the disturbance exceeds the spatial extent of the landscape because the landscape is essentially too small to characterize the effect and recovery from disturbance.

The use of ratios in both parameters permits the comparison of landscapes across a range of spatial and temporal scales. We use the parameters to describe a landscape state-space in which the temporal parameter is placed on the y axis, and the spatial parameter is displayed on the x axis. We assert that the disturbance conditions that lead to qualitatively different landscape dynamics can be identified within this state space.

The model

A simple simulation model was developed to explore landscape dynamics within the state space described above. The landscape is represented as a square grid of 100 x 100 cells. Eight vegetation classes representing seral stages are included in the model. Initially, the entire landscape is covered with mature vegetation (seral stage 8). At a fixed interval, square disturbances of a fixed size are imposed on the landscape. Disturbances can occur in all seral stages, and the effect of the disturbance is to return each disturbed cell to seral stage 1. The location of each disturbance is randomly chosen, and the disturbance events are "wrapped" so that boundary effects (Gardner *et al.* 1987) are eliminated. Disturbed sites recover deterministically through succession, passing through a seral stage at each time interval and achieving full recovery 8 time steps following the disturbance. The seral stages must follow one another sequentially, and we assume that seed sources for each stage remain present in the landscape. The disturbance-recovery process is continued for 100 time intervals.

Simulations were conducted for a set of disturbance sizes and frequencies (Table 1) chosen to represent a wide range of potential disturbance regimes within the state space. Both the recovery time (8 time steps) and spatial extent of the landscape (10,000 grid cells) remain fixed. By varying the disturbance size and frequency, a wide range of values of T and S can be explored. During the simulations, the proportion of the landscape covered by each seral stage was reported at each time step. Results for each simulation then were expressed as the mean and standard deviation over the duration of

Table 1. Spatial and temporal scales of disturbance used in a factorial simulation experiment in a 100 × 100 gridded landscape. The combinations of disturbance size and frequency yield 28 different simulations.

Spatial scale of disturbance events

Disturbance size (Number of cells)	Size of Disturbance / Size of landscape
10 × 10	0.01
50 × 50	0.25
71 × 71	0.50
86 × 86	0.75

Temporal scale of disturbance events

Disturbance return interval (time steps)	Disturbance frequency (per time step during simulation)	Return interval / Recovery time
80	0.0125	10
40	0.025	5
8	0.125	1
4	0.25	0.5
0.8	1.25	0.1
0.4	2.50	0.05
0.08	12.5	0.01

the simulation (100 time steps) of the proportion of the landscape occupied by each seral stage. This allows the persistence and constancy of each seral stage to be integrated across the landscape.

Simulation results

Qualitatively different landscape dynamics are observed under different combinations of T and S. For example, consider a disturbance regime in which the disturbance interval and recovery time are equal ($T = 1$) and the size of the disturbance is small relative to the size of the landscape ($S = 0.1$). As might be expected, the proportion (p) of the landscape in the mature stage varies between 0.9 and 1.0 in a cyclic manner (Figure 1). Similarly, the proportion of the landscape in each of the other seven seral stages varies cyclically between 0.0 and 0.1 (Figure 1). Consider another disturbance regime (Figure 2) in which the disturbance interval is short relative to the recovery time ($T = 0.1$), i.e., disturbances reoccur before disturbed sites can fully
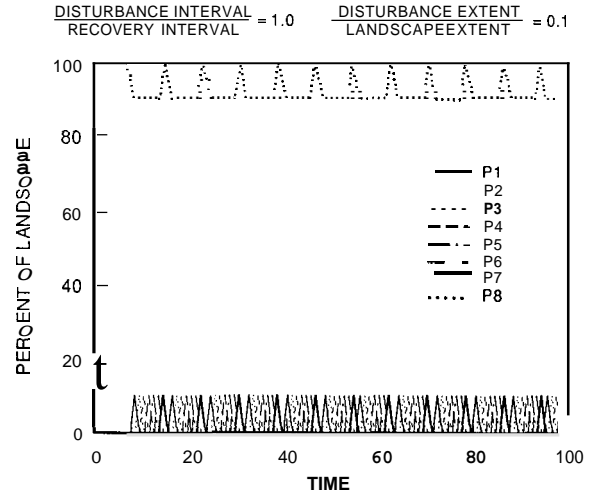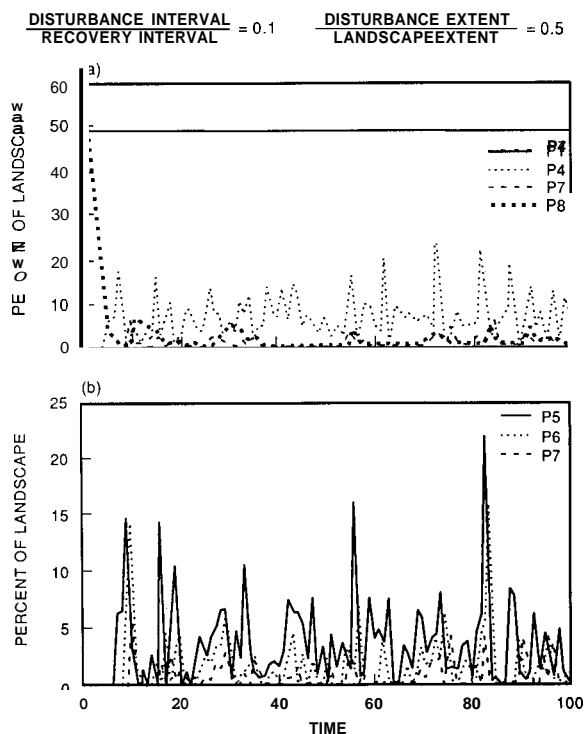

Fig. 1. Time series of the proportion *(p)* of the landscape occupied by eight seral stages during a 100 time-step simulation on a 100 × 100 landscape in which the temporal parameter $T = 1.0$ and the spatial parameter $S = 0.1$.

recover, and the size of the disturbance is large relative to the size of the landscape ($S = 0.5$). In this case, we see that the pioneer stage (seral stage 1) always occupies almost 50% of the landscape, while the mature stage (seral stage 8) varies somewhat through time but never occupies more than **5%** of the landscape (Figure 2a). The p values of the intermediate stages (e.g., seral stages *5, 6* and 7) show wide fluctuations through time (Figure 2b).

When disturbance interval is long relative to recovery time (i.e., high T) and/or disturbances are small relative to the landscape size (low S), landscapes appear to the observer as relatively constant (the upper left portion of Figure 3a). Mature vegetation (seral stage 8) covers an average of more than 50% of the landscape. Disturbances are small, recovery occurs before the next disturbance event, and the landscape appears relatively constant. The landscape seems to be well-adapted to its normal disturbance regime, i.e., it has "incorporated" the disturbance (O'Neill et al. 1986).

When disturbances are large (higher S) and relatively frequent (lower T) so that the next disturbance comes before full recovery, the initial seral stage occupies more than 50% of the landscape on the average (the lower right portion of Figure 3b). In this region of the state space, the impact of dis-
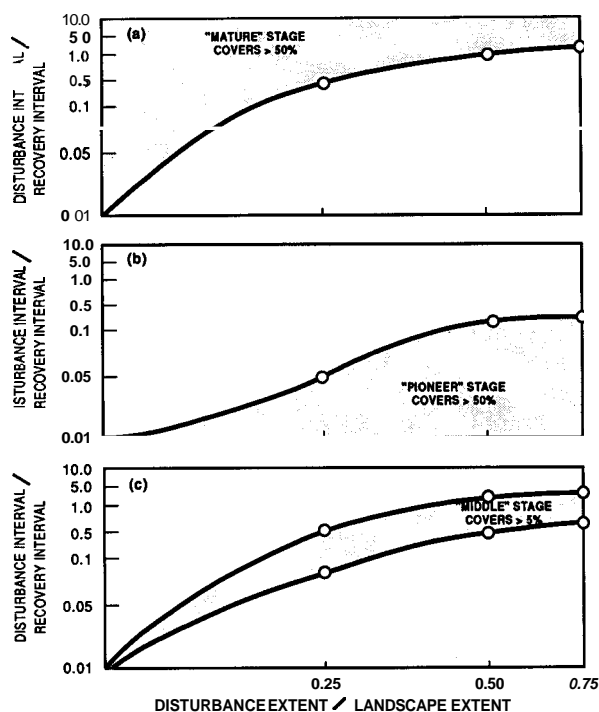
$$\frac{\text{DISTURBANCE INTERVAL}}{\text{RECOVERY INTERVAL}} = 0.1 \qquad \frac{\text{DISTURBANCE EXTENT}}{\text{LANDSCAPE EXTENT}} = 0.5$$

Fig. 2. Time series of the proportion *(p)* of the landscape occupied by (a) seral stages 1, **4, 7,** and 8, and (b) seral stages **5, 6,** and **7** during a 100-time step simulation on a 100 x 100 landscape in which the temporal parameter $T = 0.1$ and the spatial parameter $S = 0.5$.

Fig. 3. State-space diagram of the temporal and spatial parameters used to describe potential disturbance dynamics which define (a) the region in which the mature seral stage has a mean coverage > 50% of the landscape, (b) the region in which the pioneer seral stage has a mean coverage > 50% of the landscape, and (c) the region in which the intermediate seral stages have a mean coverage > 5% of the landscape.

Fig. 4. State-space diagram of the temporal and spatial parameters used to describe potential disturbance dynamics which define the regions of high and low standard deviation (SD) in the proportion of the landscape occupied by the mature seral stage during a simulation **of** 100 time steps.
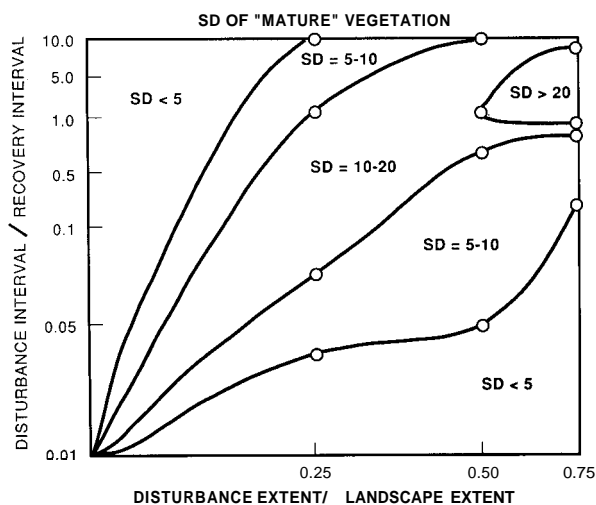
turbance would dominate our observation set. We would interpret this as a disturbance-dominated landscape.

Disturbance sizes and frequencies may also permit intermediate seral stages, such as stage **5,** to have an average cover greater than 5% of the landscape (Figure 3c). This occurs at intermediate values of T and S where many of the points on the landscape are passing through recovery stages, and the next disturbance comes about when you expect the system to recover. However, the system is still stable and always tends to return to the trajectory describing the preperturbation dynamics. This type of disturbance regime leads to very dynamic checkered landscapes.

The variability of landscape cover also provides interesting results. For example, consider the standard deviation of the proportion of the landscape covered by mature vegetation (Figure **4).** The varia-
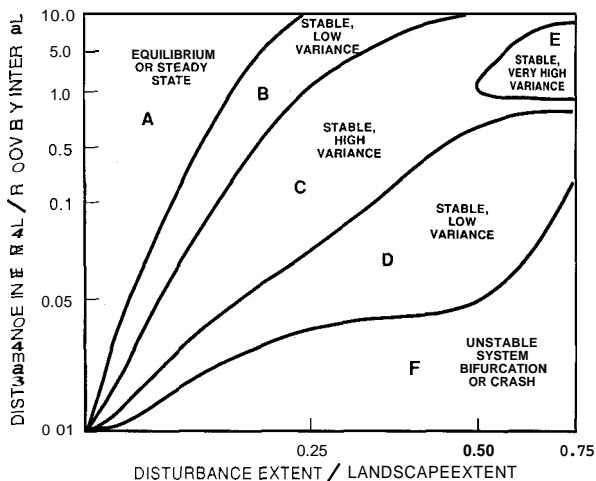
Fig. 5. State-space diagram of the temporal and spatial parameters which illustrates regions that display qualitatively different landscape dynamics.

bility is small in the upper left-hand corner (high T and low S) because the landscape is relatively undisturbed and tends to be dominated by mature vegetation (as in Figure 1). The variability also is low in the lower right-hand corner (low T and high S) because disturbances are so frequent and large that very little of the landscape contains mature vegetation (as in Figure 2). Variability in the p value of mature vegetation increases toward the center of the figure (intermediate values of T and S), making the mature vegetation appear most variable over a range from small, frequent disturbances to large but rare disturbances.

Considering the landscape dynamics (mean and variability of proportion of the landscape covered by each seral stage) observed across the state space, regions of qualitatively different landscape dynamics can be described (Figure **5**) across the continuum. Landscape equilibrium can be observed under conditions of small disturbance size and generally longer disturbance intervals relative to recovery time. **A** landscape may also appear relatively stable, exhibiting low variance in p values, if disturbances are still relatively infrequent, but disturbance size increases. We then see a stable system with low variance in which much of the landscape is still occupied by mature vegetation. This region of the state space may be comparable to the stochastic or

relative constancy defined by Botkin and Sobel (1975). The landscape may also appear stable with low variance when disturbance sizes increase even further, although the early seral stages will dominate. The landscape may be stable (sensu Loucks 1970) but show very high variance with intermediate values of S and $T,$ and show extremely high variance when disturbance size exceeds 50% of the landscape and the disturbance interval is very long. Landscapes in this region of the state space would likely be characterized as non-equilibrium systems.

Under conditions of large frequent disturbance, one of the most interesting possibilities is the potential for unstable or catastrophic change, although this is not incorporated into our model. If the disturbance is sufficiently large and/or sufficiently frequent, the landscape might not recover to the preperturbation trajectory. An alternative system might exist, and the disturbance could fundamentally change the nature of the system if the species cannot become reestablished. Subsequently, the landscape might tend to recover along a new and different trajectory.

Applications to specific landscapes

How do these types of behavior correspond to observed dynamics in landscapes? We consider several examples of landscape disturbance. Between 1972 and 1987, Yellowstone National Park (YNP) had a natural fire program in which most of the 235 fires that were ignited by lightning were allowed to burn without interference. Most fires went out without intervention before burning more than a hectare. A total of 8300 ha (approximately 1% of the Park) burned in 1981, but the area burned in other years was much less (Despain 1991). The return interval for fires of this size in the Yellowstone landscape is approximately 15 years, and the recovery time for burned forests to reach the mature stage is approximately 300 years (Romme and Knight 1982). Thus, for fires observed in Yellowstone between 1972 and 1987, the temporal parameter $T = 0.05$, the spatial parameter $S = 0.01$. This disturbance regime occurs in the lower left corner of the diagram (Figure **6**) and suggests equilibrium conditions of little
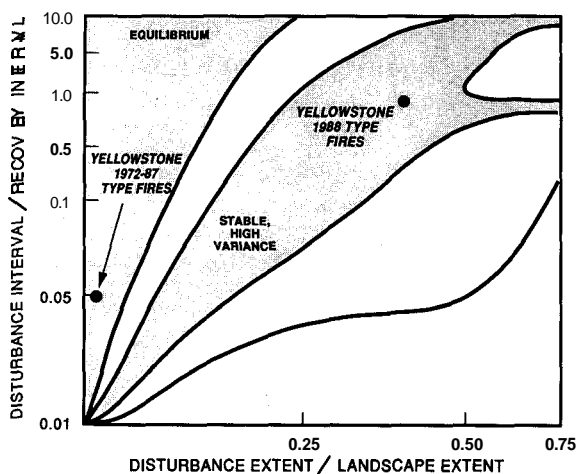
Fig. 6. State-space diagram of the temporal and spatial parameters which uses fire in Yellowstone National Park to illustrate effects of expanding the temporal scale of observations on conclusions regarding landscape dynamics.
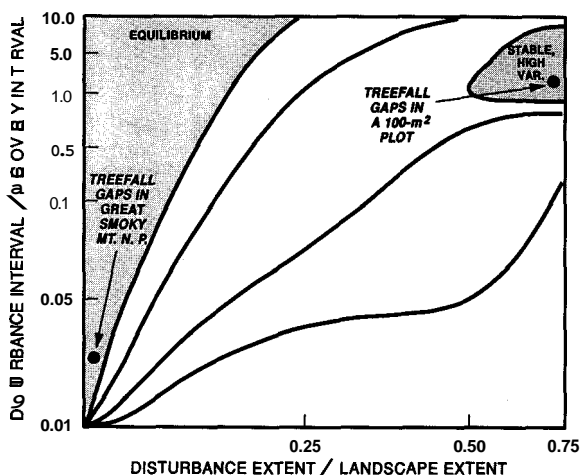

Fig. 7. State-space diagram of the temporal and spatial parameters which uses treefall gaps in deciduous forests to illustrate effects of changing the spatial scale of observations on conclusions regarding landscape dynamics.

change. In contrast, the 1988 fires that burned in YNP occurred during an extreme fire year and were the largest observed since the Park was established in 1872. Approximately 36% ($-$ 321,000 ha) of the Park was affected (Despain *et al.* 1989). The last comparable fires occurred ca. 1700, and the return interval for fires of this scale is approximately 300 yr (Romme 1982; Romme and Despain 1989). Thus, expanding the temporal scale to include fires

like those that occurred in YNP in 1988, we observe $T - 1.0$ and $S - 0.36$. This disturbance regime falls within the region of a stable landscape with high variance (Figure 6), consistent with Loucks' (1970) concept of a stationary process and Romme's (1982) failure to find a shifting-mosaic steady state in YNP.

As another example, consider the phenomenon of gap dynamics in eastern hardwood forests (e.g., Runkle 1985). At the scale of the entire Great Smoky Mountains National Park (GSMNP), Runkle estimated that treefall gaps occur every year and affect approximately 1% of the landscape annually. The recovery time for a treefall gap was estimated at $\sim$ 91 yr, the approximate time that the trees reach the canopy (Runkle 1985). Thus, for treefall gaps in the GSMNP, the temporal parameter $T -$ 0.01, and the spatial parameter $S - 0.01$. This disturbance regime occurs in the extreme lower left corner of the diagram (Figure 7) in the equilibrium region. Consider now what happens when the spatial scale is altered such that we consider treefall gaps only within a $100 \, m^2$ plot within GSMNP. The median gap size is $- 75 \, m^2$ (Runkle 1982), and we can estimate that a treefall occurs within a 10 m^2 plot every 100 years or so. Recovery time is still approximately 50 yr. Under these conditions, the temporal parameter $T - 2.0$, and the spatial parameter $S - 0.75$, bringing this disturbance regime into the region of a stable system with very high variance (Figure 7). This example illustrates nicely the dependence of our observations of landscape dynamics on the spatial extent that is considered.

Landscape dynamics with unstable or catastrophic change (i.e., the lower right corner in Figure 5) although not simulated in our model, have been observed in landscapes. In the Copper Basin of Tennessee, emissions from a copper smelter imposed large ($S = 1.0$) and essentially continuous (T approaches zero) disturbance. This led to extensive devegation and subsequent erosion losses. Erosion removed mycorrhizal spores from the soil and prevented the reinvasion of natural vegetation (Berry and Marx 1978). The basin changed from forest to sparse grasses and shrubs. A similar catastrophic change occurs in tropical forests when extensive

clearing destroys mycorrhizal spores (Fearnside 1985). Other catastrophic changes have occurred in tropical areas where deforestation introduced a new scale of perturbation. Much of the rainfall in tropical forests has its source in transpiration (Salati *et al.* 1983). Extensive deforestation in Central Africa greatly decreased transpiration. Subsequently, rainfall was insufficient to support forests and the region has undergone a catastrophic change into grasslands. In other tropical areas, extensive deforestation has permitted the invasion of an aggressive grass species, *Imperata cylindrica*, that prevents forest recovery (Richards 1966).

Landscapes that normally occupy other areas in the diagram may experience rare events that shift them to the right and downward (see Figure 5, resulting in radically different dynamics. An interesting example is provided by the California chaparral. This fire-adapted community recovers rapidly from small fires (i.e., $S \ll 1.0$ and $T < 1.0$). However, Zedler *et al.* (1983) document an unusual circumstance when a second large fire occurred on the same area within a single year. This exceeded the recovery capability of the vegetation and drastically altered the community. The recovered system was quite different from the pre-disturbance state. The system was unstable and moved to a new trajectory.

Phytoplankton community dynamics in inland lake "landscapes" also provide an example where the system can shift into the lower right region of the state space if disturbances are frequent or prolonged. In the absence of disturbance, annual succession of phytoplankton communities occurs along broadly predictable pathways due to autogenic changes in nutrient and light availability (Reynolds 1984: 317−321). Growth of algae early in the year causes the water column to become differentiated into an upper light-rich but nutrient-poor zone and a lower light-deficient but nutrient-rich zone. These zones allow the proliferation of algal taxa adapted to these specialized conditions. Physical disturbance, e.g., wind-induced vertical mixing, changes the vertical structure of the algal communities and alters the available nutrients. Because wind-induced mixing affects most, if not all, of the lake area, S is very close to 1. If the mixing
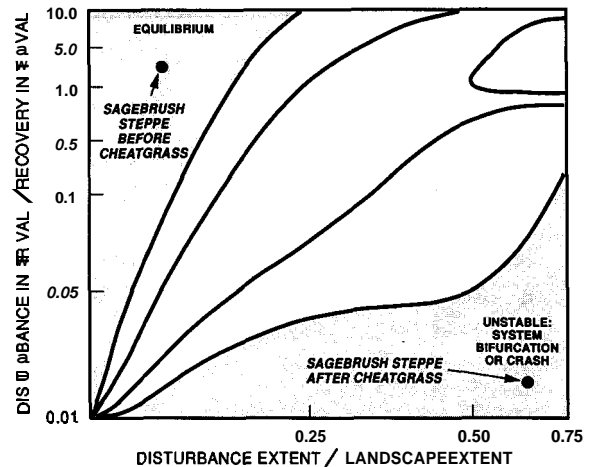

Fig. 8. State-space diagram of the temporal and spatial parameters which uses fire in sagebrush steppe before and after invasion by exotic species to illustrate the potential for bifurcation or catastrophic change.

periods are short lived (high T, then the system returns to the pre-disturbance trajectory, but often from an earlier successional stage. If the mixing periods are frequent or prolonged (low T), then the system falls into the lower right portion of the state space in Figure 5, a different trajectory is followed, and the outcome of succession is altered.

Another potential candidate for catastrophic change in response to unusual perturbations is provided by the arid sagebrush desert in the western U.S. (West 1988). The steppe is sparsely vegetated (i.e., discontinuous fuels) and dominated by perennial shrubs (e.g., *Artemisia* sp.) and bunchgrasses that are resistant to fire. The arid conditions discourage invasion of annuals into the gaps between plants where sagebrush roots are well-established. Therefore, fire is infrequent, individual fires remain small and patchy, and there is reasonable recovery (Figure 8). However, the situation changed radically with the introduction of aggressive annual weeds, especially cheatgrass (*Bromus tectorum*), by Europeans. Under conditions of drought stress, cheatgrass can expand into new areas of the steppe (F. Wagner, personal communication). Cheatgrass outcompetes the native grasses and completes its life cycle and produces seeds by early summer. The continuous and flammable fuel it creates makes the region susceptible to earlier and

more frequent fires than occurred in the past, and may of the native herbs and shrubs, including the sagebrush, are destroyed by frequent fires. Soil erosion may then be severe if the soils are without cover during the summer, resulting in a downward spiral of degradation and near permanent deterioration of the site (West 1988). This sequence of events thus causes a radical change in vegetation cover and qualifies as a catastrophic change to a new system (Figure 8).

Discussion

Disturbance regimes may be quite complex. We have not attempted to capture all aspects of this complexity, and we acknowledge that incorporating additional factors could enhance the model. The framework we have proposed predicts dynamics for a specified disturbance and landscape, but does not characterize "a landscape." Many landscapes are affected by multiple disturbances which occur at different spatial and temporal scales and which may interact. For example, Wisconsin forests are affected by fires which have a return time close to the maximum lifespan of the species present (Canham and Loucks 1984). Also affecting these forests are severe wind disturbances which have an average return time of 1000 years, which is three times the lifespan of the first-generation recovery forest (Canham and Loucks 1984). Northern coniferous forests are influenced by the interaction of parasites and lightning-caused fires (Knight 1987). A landscape affected by multiple disturbances might be described by a set of points within the state space where each point represents a particular disturbance regime. For example, large infrequent fires are the dominant influence on landscape pattern in Yellowstone National Park, but a fine-scale landscape mosaic within the dominant pattern results from small frequent fires and periodic outbreaks of the mountain pine beetle.

Another complexity is that recovery from disturbance (i.e., succession) may be influenced by the spatial extent of a disturbance, which in turn may feed back to the disturbance regime. For example, species composition may vary with patch size.

Selective cutting in northern hardwood forests favors species such as American beech, sugar maple, and eastern hemlock, whereas larger cuts favor species such as yellow birch and tuliptree (Runkle 1985). Changes in species composition or relative abundances may alter the subsequent disturbances because some species are more or less susceptible to fire, disease, blowdown or other disturbances. In southeastern deciduous forests, beech is more likely to form a treefall gap than other species (Romme and Martin 1982). A particular disturbance pattern also may alter the susceptibility of the landscape to another disturbance. Franklin and Forman (1987) demonstrate that forest cutting patterns may alter susceptibility to catastrophic windthrow. We have not incorporated all these complexities within our model, but the model can be extended to incorporate a broader suite of disturbances and feedbacks that occur within landscapes.

As spatial or temporal scale is expanded, the variance associated with environmental parameters may increase (Steele 1985), i.e., the spectrum moves from "white" to "red". Conceptually, this assumes that systems may be predictable over small areas or relatively short time periods but not necessarily at broad scales. Our simple model does not incorporate this expansion of variance with scale. That is, we have implicitly assumed constant variance in environmental forcing functions throughout the state space defined by the parameter S and T. This implies that the framework we describe cannot be expected to hold for very long time scales, when the system must be considered in an evolutionary rather than ecological context, or over very broad spatial scales (e.g., entire continents).

Our results suggest that neglecting the rare disturbances in a system may prevent an understanding of landscape dynamics as well as species persistence, energetics, soil, and nutrient relations (Franklin and Hemstrom 1981). For example all disturbances have some size distribution. Gaps formed in eastern hardwood forests followed a log-normal distribution, with many small and a few large gaps (Runkle 1982, 1985). The average size of a canopy opening was $\sim 31 m^2$, but canopy opening sizes ranged up to $1490 m^2$, with about 1% of the total land area in gaps of $> 400 m^2$ (Runkle

1982, 1985). In the Boundary Waters Canoe Area, Baker (1989a) found that the mean size of the disturbance was less important than the largest observed patch size in determining stability dynamics. We assumed disturbances of fixed size in our model. Although disturbances could have been modeled from a statistical distribution for both return and size, this would simply create a cloud of points representing each disturbance within the state-space.

The framework we propose could provide guidance for the establishment and management of natural areas in disturbance-prone landscapes. Preservation of natural areas is challenging, in part because we seek to preserve areas that are changing (White and Bratton **1990). A** variety of authors (e.g., Wright **1974;** Sullivan and Shaffer **1975;** Pickett and Thompson **1978)** have suggested that natural areas should be sufficiently large to include a mosaic of all normal stages in community development, and that natural processes of perturbation and recovery should be allowed to occur unchecked. By knowing the frequency and extent of disturbances within a landscape, the spatial extent necessary to incorporate this disturbance could be determined. Obviously, landscapes characterized by very large-scale patterns of disturbance and recovery would necessitate a much larger natural area that might be required under systems in which perturbations are small and frequent. However, it is important to remember that our projections only address the dynamics of seral stages, and the use of other attributes (e.g., species, biomass, etc.) may give different results.

There is no reserve size that can guarantee landscape equilibrium. However, increasing reserve size should decrease the probability of a dramatic shift in landscape dynamics due to a rare disturbance event. A distribution describing the probability of occurrence of disturbances of different size could be constructed for a given landscape. If the frequency distribution of disturbance size extends asymptotically to infinity, then no landscape will be sufficiently large to incorporate all disturbances. Note that this will occur if the temporal scale of observation is extended indefinitely. However, the shape of the probability distribution could be used to estimate the likelihood of extremely large disturbance events altering the landscape.

Our results also have important implications regarding global climate change because the interaction between climate and disturbance regimes influences landscape patterns (Graham *et al.* **1990).** Past climatic changes of small magnitude have caused significant changes in fire regimes in forested landscapes (Hemstrom and Franklin **1982;** Clark **1988, 1990).** Global warming may result in an increase in the frequency of dry years and hence an increase in the size or frequency of fire (Sandenburgh *et al.* **1987;** Flannigan and Harrington **1988;** Romme and Turner **1991).** One could explore the implications of climate-induced changes in a disturbance regime by locating the current position of a landscape in Figure **5,** then plotting a potential future position within the state space under a new disturbance regime. In this manner, the potential for a qualitative shift in landscape dynamics, e.g., from equilibrium to stable with high variance, could be identified. Alternatively, a landscape might be able to sustain a fairly substantial change in disturbance regime and remain within the same region of dynamics.

Much of the controversy surrounding concepts of landscape equilibrium can be eliminated with the explicit consideration of the spatial scales of disturbance and the landscape and the temporal scales of disturbance and recovery. Landscapes can exhibit a variety of behaviors under different disturbance regimes, and the same landscape may shift among different regions of behavior. Landscapes that traditionally are considered as being in equilibrium are characterized by small and infrequent disturbance and rapid recovery. Stable systems with high variance are characterized by intermediate size and frequency of disturbance and intermediate rates of recovery. Potentially unstable systems are characterized by large and frequent disturbance and slow recovery. In these landscapes, a system crash or bifurcation to a qualitatively different system is possible. The framework we propose permits the prediction of disturbance conditions that lead to qualitatively different landscape dynamics and demonstrates the scale-dependent nature of concepts of landscape equilibrium. Our results demon-

strate that conclusions regarding landscape equilibrium are appropriate only for a specified spatial and temporal scale. Failure to recognize this dependence can lead to sharply different interpretations about the same dynamics.

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